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Landscape Connectivity: Different Functions at Different Scales

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Connectivity is more than corridors, and corridors are more than linear strips of habitat. Rather, connectivity involves linkages of habitats, species, communities, and ecological processes at spatial scales ranging from fencerows to biomes, and at temporal scales ranging from daily movements of animals to migrations of floras and faunas as climate changes over centuries and millennia. Any piece of land or water may be either a corridor or a barrier to dispersal, depending on the life histories of the organisms concerned. Biogeographers use the term "filters" to describe areas through which organisms disperse, because species that are poor at dispersing through the habitats involved will be selectively removed. Human activity may either increase connectivity (favoring biological invasions) or decrease connectivity (favoring extinction of isolated populations). Roads are particularly troublesome as barriers, conduits for exotic invasions, and mortality sinks. A general recommendation for conservation of biological diversity is to maintain landscapes with high connectivity of natural habitats, but with low connectivity of artificial habitats such as roadsides, clearcuts, and agricultural fields. Special attention should be given to the needs of species that require broad corridors of habitat with little disturbance by humans, to minimizing opportunities for spread of exotic species, and to maintaining corridors at regional and continental scales to accommodate migration of all native species as climate changes.

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Connectivity is more than corridors, and corridors are more than linear strips of habitat. Rather, connectivity involves linkages of habitats, species, communities, and ecological processes at spatial scales ranging from fencerows to biomes, and at temporal scales ranging from daily movements of animals to migrations of floras and faunas as climate changes over centuries and millennia. Any piece of land or water may be either a corridor or a barrier to dispersal, depending on the life histories of the organisms concerned. Biogeographers use the term "filters" to describe areas through which organisms disperse, because species that are poor at dispersing through the habitats involved will be selectively removed. Human activity may either increase connectivity (favoring biological invasions) or decrease connectivity (favoring extinction of isolated populations). Roads are particularly troublesome as barriers, conduits for exotic invasions, and mortality sinks. A general recommendation for conservation of biological diversity is to maintain landscapes with high connectivity of natural habitats, but with low connectivity of artificial habitats such as roadsides, clearcuts, and agricultural fields. Special attention should be given to the needs of species that require broad corridors of habitat with little disturbance by humans, to minimizing opportunities for spread of exotic species, and to maintaining corridors at regional and continental scales to accommodate migration of all native species as climate changes.

INTRODUCTION

The subject of this workshop is landscape linkages, which we might define as linear corridors of habitat that physically connect larger habitat patches in a landscape mosaic. In this paper, I address a broad concept of connectivity, which involves linkages of habitats, species, communities, and ecological processes at multiple spatial and temporal scales. I argue that because ecological processes and elements of biological diversity occur at a variety of scales, a comprehensive strategy to conserve these processes and elements must also be scale-pluralistic.

Many of the most significant human effects on biodiversity involve changes in the connectivity of biological phenomena. Human activities may either reduce or increase connectivity. We have created artificial barriers to species dispersal in many instances, whereas in other cases we have eliminated natural

barriers. In the former situation, isolated populations become more vulnerable to extinction due to reduced access to resources, genetic deterioration, increased susceptibility to environmental catastrophes and demographic accidents, and other problems (Harris 1984, Soule' 1987). In the latter situation, we make it easier for exotic organisms to invade indigenous communities. The end result of this process is a homogenization of floras and faunas, an example of which Crosby (1986) called "ecological imperialism": the conversion to a biological neo-Europe of every region settled by people of European descent.

PROCESSES OF MOVEMENT AND DISPERSAL

In biology, motion occurs at many levels of organization. Of most relevance to conservation biology is the movement of organisms across landscapes (and seascapes), and of alleles (genes) within and among populations of organisms. Many animals make daily and seasonal movements to meet life-history needs, and depend upon corridors or "stepping-stones" of appropriate habitat to do so. "Dispersal," on the other hand, refers to the movement of organisms away from their place of origin; the movement of alleles due to dispersal of gametes or offspring is called gene flow (Brown and Gibson 1983). It is particularly critical that avenues for dispersal be maintained in times of climate change, when organisms must track shifting habitat conditions.

"One of the striking features of life on earth is its lack of uniformity in distribution" (Cox and Moore 1985). Biodiversity is a dynamic consequence of dispersal and isolation. If we look at any local site on Earth, except for oceanic islands and a few island-like continental habitats, the overwhelming majority of species we see came from somewhere else. Only a small number of species, if any, evolved there in situ. As we enlarge our area of observation, a greater number of species are endemic to that area, i.e., they are found nowhere else. The island continent of Australia has a large proportion of endemic species (and now, many human-introduced exotics). In many cases, endemics are thought to have evolved within the areas in which they are found today. In other (probably fewer) cases, an endemic species may once have been widespread, then contracted in distribution to its present range. For any area, including islands, endemics evolved from ancestors that originated elsewhere, ultimately going back to the primordial and unknown place where life began. Thus, dispersal followed by at least partial isolation and subsequent differentiation into new species, is responsible for biodiversity.

<u>Corridors, barriers, and filters</u>. Of great import to conservation biology is the fact that organisms differ in their dispersal capacities. Most birds, bats, and flying insects are mobile, whereas terrestrial snails and flightless insects are quite sedentary. Plants that have their seeds dispersed by birds or wind may be very mobile, whereas forest wildflowers dispersed

by ants are not. Furthermore, a corridor to one species is a barrier to another. A strip of forest through agricultural land, for example, would provide a corridor for dispersal of forest animals that avoid clearings, but would form a barrier to movement for species such as the meadow vole. A river facilitates movement of fish, but may form a barrier for many terrestrial organisms. Related species or subspecies often are found on opposite sides of major rivers (Hesse et al. 1937). Some tropical birds, despite their powers of flight, have psychological barriers to crossing even narrow water gaps (Diamond 1975).

Different species disperse through different types of habitat. Biogeographers usually limit their use of the term "corridor" to broad, internally heterogeneous swaths of habitat that permit the direct spread of many or most taxa from one region to another (Brown and Gibson 1983). "Filters" (sensu Simpson 1940), on the other hand, are dispersal routes containing a more limited habitat spectrum, and through which certain species pass and others are excluded. A clearcut, for example, is a filter which some forest mammals (such as black bear) may cross but others such as pine marten avoid (Soutiere 1979). When organisms are faced with crossing totally unsuitable habitats, such as terrestrial amphibians making their way to oceanic islands or a Florida panther trying to cross downtown Miami, such chance movement is called "sweepstakes dispersal." Unfortunately, our knowledge of what constitutes a barrier or a corridor for various species is extremely limited. We do not even have adequate models for dispersal of animals or plants through heterogeneous environments; most existing models of dispersal (for example, based on diffusion equations) assume a homogeneous environment and a random walk (Lubina and Levin 1988).

The conservation strategy that emerges from these considerations is one that seeks to optimize the width and variety of natural habitats in landscape linkages, so that the full spectrum of native species will be able to move between natural areas in the regional landscape (Noss and Harris 1986, Noss 1987a). Narrow corridors, or corridors comprising only one kind of habitat, are less useful. A narrow corridor may be composed entirely of edge habitat that is not suitable for forest interior species. Riparian habitats are often suggested as dispersal corridors, but may not be useful for species of dry, upland habitats (Forman 1983). An ideal corridor might encompass the entire topographic gradient and habitat spectrum from river to ridgetop. But in some landscapes, wide corridors are no longer available and cannot, in the short term, be restored. In such cases, multiple corridors ("networks") may collectively encompass the full range of native habitats, and also insure against destruction of single corridors by catastrophic disturbances (Forman and Godron 1981).

The flip side of the corridor or network strategy is to minimize

barriers. Urban areas, agricultural fields, clearcuts, and roads conspire to make dispersal difficult for all but the "weediest," most vagile species in the modern landscape, and should be restricted from corridors as much as possible. Roads are particularly troublesome, as they now cover so much of the landscape and are filters through which many organisms do not successfully pass. Oxley et al. (1974) found that small forest mammals in southern Canada rarely ventured onto road surfaces when the width of the road clearance exceeded 20 m. In Germany, several species of forest-dwelling carabid beetles and mice rarely or never crossed two-lane roads; even a small, unpaved forest road closed to public traffic was a barrier (Mader 1984). Surprisingly, even mammals of open habitats such as the deserts may rarely cross highways (Garland and Bradley 1984). For species restricted from crossing roads, a road effectively cuts a population in half and makes it more vulnerable to extinction. Moreover, climate change, whether natural or anthropogenic, will intensify the deleterious effects of roads and other artificial barriers, as animals (and the plants they disperse) are prevented from tracking shifting climate zones (Peters and Darling 1985). Closing roads, minimizing new road construction, and building underpasses and viaducts are some of the strategies that have been offered to address this problem (Noss 1987b, Harris and Gallagher 1989).

SPATIOTEMPORAL SCALES OF CONCERN

An important realization of modern conservation biology is that conservation problems exist at many different spatiotemporal scales and levels of biological organization. Similarly, conservation strategies are applicable at multiple scales (Noss 1990). It is critical, of course, that the proposed solution match the scale and nature of the problem. Maintaining wooded fencerows may help white-footed mice travel among woodlots, but won't do much for wolves. A strategy that serves to maintain biodiversity in the short term (i.e., a few years) may fail to maintain viable populations and ecological integrity over a longer time span.

What is the optimal scale for planning and managing habitat connectivity? It depends on the biota under consideration, and the goals and objectives of the conservation strategy.

The fencerow scale. Gray Merriam and his students at Carleton University in Ontario have convincingly demonstrated the value of fencerows to small mammals in agricultural landscapes. Local extinctions of white-footed mice and chipmunks are high in small, isolated woodlots, but fencerows permit frequent recolonization and the metapopulation persists (Wegner and Merriam 1979, Fahrig and Merriam 1985, Henderson et al. 1985, Merriam 1988). Fencerows appear to allow mice to move between woodlots with less risk of predation than if they cross open fields. Even birds may depend on habitat corridors. In the Netherlands, the number of

forest-interior birds in woodlots is significantly related to the density of connecting elements, such as wooded banks and tree rows (van Dorp and Opdam 1987). To avoid predation in fall from migrating hawks, blue jays in Wisconsin fly over fencerows instead of open fields and dive into cover if attacked (Johnson and Adkisson 1985). Many species of birds and mammals (plus a snake) have been noted to use hedgerows for movement across a landscape, whereas the same hedgerows block movement of other animals, such as cows (Forman and Baudry 1984). A disadvantage of fencerows and hedgerows is that they are narrow and therefore entirely edge habitat (i.e., "line" corridors instead of "strip" corridors; Forman and Godron 1981). Some interior forest species will be unable to use these narrow corridors, and weedy, opportunistic species of edge habitats may benefit at their expense (Simberloff and Cox 1987).

The landscape mosaic scale. We usually think of corridors in terms of discrete, linear strips from one habitat patch to another. But as noted above, the use of the term "corridor" by biogeographers is much broader. Any area of habitat through which an animal or plant propagule has a high probability of moving may be considered a corridor or linkage. Wide-ranging mammals such as bears and mountain lions require such corridors on a daily basis to meet their needs for food, water, and shelter, and may roam tens of miles in a 24-hour period. Riparian and topographic ridge systems are followed routinely by these species (Harris 1985). Amphibians and migratory ungulates use corridors for seasonal movements across the landscape mosaic, as do other animals that require a variety of habitats for different stages in their life cycles. Connectivity of the landscape mosaic is absolutely necessary for these species to survive. Furthermore, disturbances periodically make parts of the landscape uninhabitable. Corridors fulfill a "fire-escape" function by permitting animals to flee disturbance, and then aid in the recolonization of the recovering site by plants and animals.

Another kind of connectivity has to do with continuity of habitats and processes along environmental gradients. Too often, ecologists and conservationists have looked at habitats as separate entities, whereas in reality they are interacting, functional components of the landscape ecosystem (Noss 1987c). Plant species usually are distributed independently along gradients, such that species diversity can be appreciated only by considering the gradient as a whole. Disturbances and other ecological processes interact with gradients of soil and moisture to determine the distribution of species. For example, in pinelands of the Gulf coastal plain, fires sweep down gradual slopes and prune back wetland shrubs that otherwise would encroach from adjacent swamps. In the process, these fires maintain an open, herb bog community with an extremely diverse flora, including many insectivorous plants. If fires are

suppressed, or if firelanes disrupt the hydrology of the slope-moisture gradient, its unique flora is destroyed (Noss and Harris 1989). Thus, connectivity of process is just as important to maintain as connectivity of habitat.

Regional and continental scales. A remarkable development in conservation over the last decade has been the emergence, in many parts of the world, of ambitious strategies to interconnect nature reserves into regional networks (Harris and Gallagher 1989). An example of a comprehensive regional network is one proposed for the state of Florida, plus Okefenokee Swamp in adjacent Georgia (Fig. 1; Noss 1987b). Noss and Harris (1986), Harris (1988), and Harris and Gallagher (1989) discussed in greater detail many of the specific linkages in this system. Although the statewide network is admittedly an idealistic strategy, particularly in a state with over 1000 new human residents each day, it has been endorsed by several environmental groups and the Florida Department of Natural Resources (in principle). The state of Florida, the federal government, and The Nature Conservancy have acquired several key linkages in the network, and other corridor acquisitions are pending (Noss 1987b).

There is a need to think even bigger than statewide networks, which is especially evident when we enlarge our temporal view to centuries and millennia. Changes in climate in the near future may be much more rapid than most past changes, perhaps at the scale of decades. Even natural rates of climate change are a threat to species in fragmented landscapes. Although dispersal barriers exist in nature, habitat fragmentation has greatly increased the number of barriers for most native species. In the past, biogeographic corridors on massive scales, such as the Bering land bridge, the isthmus of Panama, and the Gulf coastal savanna, have been critical determinants of present patterns of biodiversity (Simpson 1940, 1965, Brown and Gibson 1983, Harris 1985). Conservation biologists have proposed the establishment of corridors on regional and continental scales to permit the shifting of floras and faunas in response to global climate change (Hunter et al. 1988, Peters 1988). Proposed regional linkages include a network of protected areas paralleling the Appalachian Trail (Sayen 1987, Hunter et al. 1988), and a network of national parks, national forests, and national wildlife refuges in the western United States (Salwasser et al. 1987). Strong differences of opinion exist on how much human activity (e.g., clearcutting, roads) can exist within units of a network without seriously limiting its viability for wildlife. No longer is there any significant argument, however, over the need for such networks.

TO ENHANCE OR NOT TO ENHANCE

So far, I have discussed movement and dispersal of organisms as something that should be encouraged. The problems addressed in

this symposium are related to fragmentation of habitats and other artificial limitations of natural movement patterns. But at the same time that human activity has restricted opportunities for movement of many taxa, it has abetted movement of other taxa. Floras and faunas that once were distinct and endemic are now dominated by exotics and cosmopolitan weeds. The cause of this biological pollution has been human transportation that facilitates spread of certain species far beyond their natural dispersal capacities and habitat modification that favors weedy invaders, such as annual plants, over native flora and fauna (Elton 1958, Mooney and Drake 1986). The same road that restricts movement of some animal species may encourage movement of others. The meadow vole, for example, rapidly extended its range into central Illinois when a superhighway with grassy verges was constructed (Getz et al. 1978), and many weedy and exotic plants spread along roadsides.

A curious thing about biological invasions is that they often result in a community with more species than the original (Mooney 1988, Vitousek 1988). Should conservationists therefore applaud the spread of exotics? Not if we recognize that enhancement of species richness at a local scale can mean loss of species richness at a global scale, as sensitive endemics are lost and weeds prosper everywhere. Many of the Mediterranean-climate regions of the world, which once had distinct endemic floras, are now dominated by the same species of plants. Ecosystem-level diversity declines as distinct communities are lost; the inevitable result is global homogenization (Mooney 1988). The lesson for conservationists is that limiting dispersal of opportunistic, invasive organisms (exotic or native) is as important as enhancing dispersal of sensitive native taxa, if the goal is to maintain native biodiversity and ecological integrity. Thus, a suitable goal may be to optimize the connectivity of natural habitats in the landscape, but at the same time minimize the connectivity of artificial habitats such as clearcuts, agricultural fields, and roadsides.

CONCLUSION

Most of the controversy that has surrounded the corridor issue has involved concerns that the wrong species (i.e., weeds) might benefit and that the costs of establishing corridors are so high that money would be better spent on habitat containing concentrations of endangered species (Simberloff and Cox 1987). Much of this concern has evaporated with the realization that small, isolated reserves will not maintain viable populations of many taxa in the long term, that climate change demands that organisms be able to move large distances over time, and that society has sufficient funds to buy both endangered species habitat and corridors -- if it can find the will (Noss 1987a, Harris and Gallagher 1989).

Much of the discussion about corridors leaves the impression that

we are constructing something new on the landscape. We talk of "establishing" corridors, rather than of "maintaining" corridors. In fact, an engineering approach to corridors is necessary chiefly when roads are in the way, and underpasses, tunnels, or viaducts must be constructed so that animals can pass underneath them. Habitat restoration is also needed in many cases, sometimes on a massive scale. But the corridor strategy is fundamentally an attempt to maintain or restore natural landscape connectivity, not to build connections between naturally isolated habitats (Noss 1987a).

Critics point out that conservationists have not proven that any particular corridor strategy will work, or more precisely, that the null hypothesis of no effect of corridors has not been falsified (H. Salwasser, pers. comm.). But null hypotheses in ecology are not straightforward. In this instance, two basic alternative null hypotheses are possible: (1) there is no effect of corridors; or (2) there is no effect of fragmentation, i.e., of eliminating natural corridors. Testing the second null hypothesis is arguably the more prudent course, as it errs on the side of preservation. We know that natural landscapes are fundamentally interconnected, and that connectivity declines with human modification of the landscape (Godron and Forman 1983, Noss 1987a). Furthermore, the null hypothesis of no effect of fragmentation has been tested and falsified, repeatedly, in many parts of the world. The effects of fragmentation can be devastating (Wilcove et al. 1986). In general, then, we can reject the null hypothesis of no effect of fragmentation and consider maintenance of habitat corridors a viable option for conservation. We have a lot to learn, however, about the management of specific corridors for biodiversity and human use combined.

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Figure 1. A proposed network of preserves, buffer zones, and corridors for Florida. Adapted from Noss (1987b).

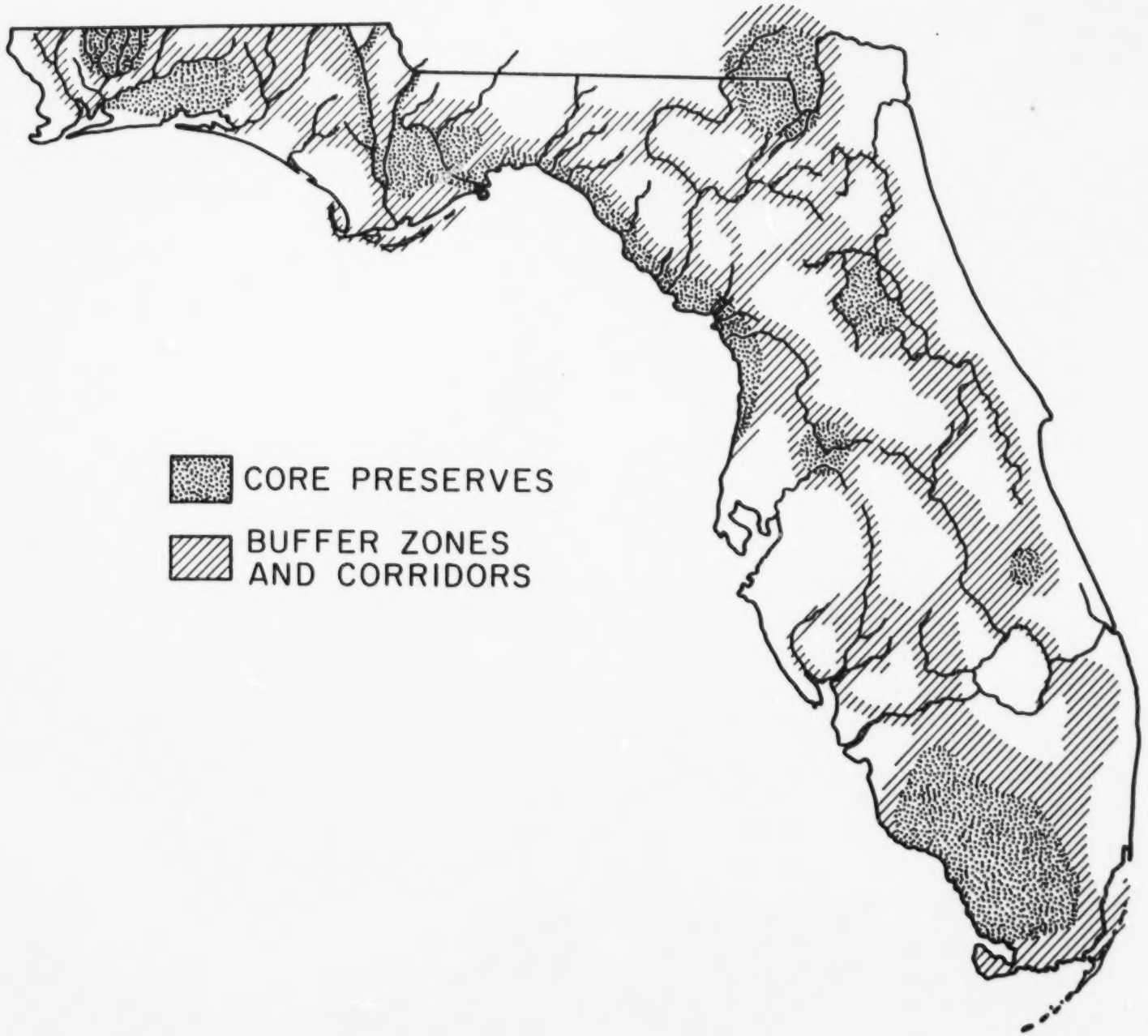

Fig. 1